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### PHYLOGENY OF SOME CALLIMOMID GENERA (PARASITIC HYMENOPTERA)<sup>1</sup>

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#### INTRODUCTION

This is a study of the phylogenetic positions of several genera and subfamilies of the Callimomidae. I have not had access to the tropical members of the family, and thus this study will not be complete, but it may give a better understanding of the evolution of the genera and subfamilies which have been considered.

In considering the phylogeny of any of the families of the Chalcidoidea, one is handicapped, because no one has carefully worked out the evolution of the families which constitute that

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group. As is well known, the chalcidoids are probably as specialized or more specialized than any of the other large groups of the Hymenoptera, but one cannot always be sure whether obvious simplicity denotes primitiveness or specialization.

However, one also finds this an interesting group with which to work, because of the variety of habits exhibited. Parasitism is the outstanding phenomenon common to the family as a whole. The wasps are parasitic upon several orders of insects in the egg, larval, pupal, and even newly emerged adult stages. Some genera or subfamilies seem to be highly specialized in their choice, while others attack widely different hosts. Phytophagy is known to occur in at least two subfamilies with possibilities that the phenomenon occurs in others. There are also indications of parthenogenesis and polyembryony in the family.

The group with which we are dealing is one of the families of the Chalcidoidea (or a subfamily of the Chalcididæ as older workers and even many present day workers call it). The name Callimomidæ, based on the oldest generic name in the family, seems preferable to the name Torymidæ which is also applied to the group. I have used the currently accepted generic names practically without critical revision.

As for the affinities of the Callimomidæ, Ashmead (1896) and others, have suggested that this group was derived from the cynipoids, and there certainly are obvious affinities between the two groups. It has likewise been suggested that the Callimomidæ are most closely related to the Eurytomidæ, Chalcididæ, and Agionidæ among the chalcidoids. Before one can be too specific on these points, a great deal more careful work must be done upon all groups concerned.

In my collection there are between 20,000 and 25,000 insects which have been collected from the following states: Indiana, Wisconsin, Michigan, Iowa, Illinois, Pennsylvania, New York, Ohio, Minnesota, Missouri, Massachusetts, Mississippi, Alabama, Arkansas, Tennessee, Kentucky, Florida, Louisiana, Texas, North and South Carolina, New Mexico, Colorado, and California. I have also some collections from near Berlin, Germany, and many collections from the central and western parts of Mexico.

The following is the material upon which this study has been based:

Callimominæ: *Callimome*, *Diomorus*, *Ecedauma*.

Monodontomerinæ: *Monodontomerus*, *Zaglyptonotus*, *Ditropin-itus*, and *Eridontomerus*.

Ormyrinæ: *Ormyrus* and *Monobaeus*.

Megastigminæ: *Megastigmus*.

Podagrioninæ: *Podagrion*.

I have been unable to include either the Idarinæ or the Erimerinæ because of lack of material. The latter group appears to be close to Monodontomerinae, and judging from published descriptions doubtfully possesses subfamily rank. The primary distinguishing feature of the Erimerinæ is the possession of one rather than two spurs on the hind tibia, and this of course may have originated through a single minor mutation.

#### PART I. PHYLOGENETIC CONSIDERATIONS

In the recognition of phylogenetic relationships within this group, the following morphologic and biologic characteristics were employed:

##### *Morphologic Characteristics:*

1. The thorax: size in relation to the body; degree of fusion of plates; shape and sculpture.
2. The antenna: length in relation to the body; tendency toward, or absence of clubbing; relative size and shape of segments.
3. The abdomen: size of plates; distinctness of segmentation; presence or absence of the tendency for a petiole to develop; presence or absence of compression and sculpture; and general abdominal shape.
4. The ovipositor: length of the external parts of the ovipositor and the length of the ventral valves in comparison to the body; and in some cases, the tendency for the ovipositor to coil upon itself proximally.
5. The legs: whether or not the femora are enlarged, and the presence or absence of spines on the femora.

##### *Biologic Characteristics:*

1. Host relations: whether the insects are parasitic, phytophagous, or both, and the number of orders, families, and genera which constitute the hosts of each group.
2. Type of parasitism involved: upon which stage or stages of their hosts each group is parasitic, and the amount of restriction

shown by each group. Also whether the insects are primary or secondary parasites, or both.

Although the drawings here reproduced are primarily those of female structures, the observations have been taken from both male and female. The female insect was used in most cases because more structures were available for study, and in most instances, more females are represented in a series than males.

### *The Thorax*

The thorax of even the most primitive of the Callimomidae is highly modified in comparison with that of some of the lower Hymenoptera.

In the sawflies, according to Snodgrass (1911), the thorax is rather loosely put together, and the three segments approach each other in size; although even in these primitive Hymenoptera the mesothorax is becoming larger. The postnotum of the meso- and sometimes of the methathorax, is distinguishable, and the pleura of these segments are divided by plural sutures into an epimeron and an episternum. The notum of the mesothorax is either a simple plate, or divided into an anterior and posterior part.

The thorax of the higher Hymenoptera which, according to Snodgrass, was derived from a thorax something like that found in the sawflies, has undergone extreme modification. In general the thorax of these higher Hymenoptera has become more compact by the dropping out of parts, although there has been an increase in size of the mesothorax. The postnotum of both meso- and metathorax has presumably become invaginated into the thorax. The notum of the mesothorax is modified by the formation of sutures; so that in some cases this may contain as many as five plates. The divided mesopleuron of the lower Hymenoptera becomes fused into a single plate in these higher groups, but in some cases there is a secondary suture developed which divides the pleuron into dorsal and ventral parts. An extra plate, the prepectus, is sometimes formed, which is probably derived from the mesopleuron and the mesosternum.

Because of this extreme modification of the chalcidoid thorax, there is current in the literature many misapplications of terms. One of these concerns a notch "above the middle on the mesepi-

sternum." This characteristic supposedly separates the Callimominae from the other subfamilies of the Callimomidae. In reality this notch is not on the mesepisternum, but on the mesepimeron, and there is no reason for the continuance of an error which apparently originated with Ashmead.

The following phylogenetic criteria were used in the present study of the thorax:

1. A thorax that is greatly shortened in proportion to the whole body length is specialized. Compression or flattening of the thorax is a specialization.
2. Fusion of sutures is an indication of specialization.
3. The presence of a secondary suture on the mesepimeron is possibly primitive in this family. It is present where the fusion of other sutures is at a minimum. I have designated the plate that this suture cuts off as the secondary epimeral plate.
4. Presence of well-developed sculpture or punctations is evidence of specialization.
5. A dorsally truncate pronotum is a specialized structure.
6. A greatly enlarged propodeum is a specialization. This structure represents the first abdominal segment which has become attached to the thorax.

**Callimominæ:** In *Callimome* (Fig. 5) the thorax is elongate with no decided tendency for shortening or flattening. The notum is not truncate dorsally, the secondary epimeral suture is definite, and there is practically no inclination for sutures to fuse. Some of the larger species possess definite punctations. In a few species, the thorax is somewhat humped, while in others, the parapsidal grooves show some inclination to fuse. The propodeum is of normal size.

In thoracic features, *Diomorus* is essentially the same as *Callimome*.

In *Ecdauma* (Fig. 6), however, modifications occur. The thorax is elongate and considerably flattened, and the propodeum is more enlarged. Excessive punctations are absent.

*Callimome* and *Diomorus*, then, seem to possess a comparatively primitive thorax, while in *Ecdauma* it is somewhat modified.

**Monodontomerinæ:** In all this subfamily, the secondary epimeral suture, although still distinguishable, becomes obscure. The

thorax is not especially reduced in proportion to the body, the parapsidal grooves are poorly developed in most genera, and the pronotum is somewhat truncate dorsally.

In all species of *Monodontomerus*, (Fig. 8) the propodeum is either striate or rugose, and there is extreme rugosity in one species. In this same species, the pleural suture is lost, but in other species this suture is evident. The thorax is humped in most species, while the propodeum is of normal size and not truncate.

*Zaglyptonotus* (Fig. 12) differs from *Monodontomerus* primarily in the following: The pleural suture is evident, the thorax is not humped, and the propodeum is not excessively rugose.

In *Eridontomerus* (Fig. 10) and *Ditropinotus* (Fig. 11) a peculiar sculpture is present which is remarkably alike in both genera. The parapsidal grooves are somewhat more evident than in the other genera of this subfamily, while the pronotum dorsally is somewhat more truncate. The thorax of *Eridontomerus* is somewhat flattened, while in both genera the propodeum is truncate.

All these genera of the Monodontomerinae seem somewhat modified in thoracic features.

**Megastigminae:** The thoracic color of *Megastigmus* (Fig. 13) makes it difficult for one to detect poorly defined sutures. The parapsidal grooves are clear cut, and other sutures on the thoracic dorsum are evident. The pronotum of this genus is comparatively more enlarged dorsally than in any other genus of the family. Because of this enlarged pronotum and the normal sized propodeum, the thorax is not reduced in proportion to the whole body. The thorax is usually well arched, and seems to be somewhat compressed. The pleural suture is lost in some species, and the presence of a secondary epimeral suture is doubtful. This thorax seems to be some departure from the primitive type.

**Ormyrinae:** The genus *Ormyrus* (Fig. 9) differs markedly from the previously described groups in thoracic characters. The parapsidal grooves are obscure in some species and entirely absent in others. There is no indication of a secondary epimeral suture, and although the pleural suture is evident, most of the other sutures show inclination to disappear. The propodeum

and pronotum are truncate, while the scutellum in many cases extends out over the propodeum. The thorax is extremely reduced in proportion to the whole body, and considerably humped.

While the above description applies primarily to *Ormyrus*, it will fit *Monobæus* with slight modification. In this genus, the parapsidal grooves while still obscure, are more evident than in most species of *Ormyrus*. However, the thorax is more humped.

The thoraces of this whole subfamily seem to be highly specialized.

**Podagrioninæ:** *Podagrion* (Fig. 7) likewise possesses a highly specialized thorax, but the specialization is quite different from that in the Ormyrinæ. The thorax is uniformly sculptured, the parapsidal grooves are faint to absent, and the presence of a secondary epimeral suture is doubtful. The pleural suture is absent, while the propodeum is enormously enlarged. Because of the enlarged propodeum, the thorax is elongate in proportion to the body. The thorax of *Podagrion* is also decidedly flattened.

**Discussion of the thorax:** From thoracic data alone, we have some guide as to the relationship between the different genera and subfamilies. *Callimome* and *Diomorus* are certainly closely related since these genera do not differ essentially in any thoracic character. *Ecdauma*, while obviously related to these two genera, is more modified.

All the genera of the Monodontomerinæ seem rather closely related with *Ditropinitus* and *Eridontomerus* possibly closer than any of the others. This whole subfamily seems related to the Callimominæ in the fact that the secondary epimeral suture is distinguishable in both groups, while in the other subfamilies it is barely discernible to absent. Evident parapsidal grooves (less evident in the Monodontomerinæ) may be other evidences of relationship between the two subfamilies, as is the medium sized propodeum found in both groups.

That *Megastigmus* (of the Megastigminæ) is related to the Callimominæ is evidenced by the following: The parapsidal grooves are clear cut in *Megastigmus* and in many species of the Callimominæ, the propodeum is medium sized in both groups, and the pronotum dorsally is elongate and not truncate.

*Podagrion* (Podagrioninæ) resembles *Ecdauma* (Callimominæ)

in possessing an elongate propodeum, and a thorax that is distinctly flattened. *Podagrion* has a sculpture that is remarkably similar to that in *Ditropinitus* and *Eridontomerus* of the Monodontomerinæ. In all the Monodontomerinæ and *Podagrion*, the pronotum dorsally is more or less truncate.

The Ormyrinæ do not seem to be closely related to any of the other groups in thoracic features, since the thorax is remarkably shortened, the parapsidal grooves are in most cases lost, sculpture is absent, and there is no sign of a secondary epimeral suture.

#### *The Antenna*

The antennæ of this family are quite variable, but in number of segments they are remarkably constant. All the antennæ have thirteen segments, but at times the distal three segments are hard to distinguish, presumably because of fusion. The first segment is commonly known as the scape, the second as the pectid, and the invariably small third segment as a ring joint. Sometimes the fourth segment is also reduced to the state of a ring joint. The more elongate segments which follow the ring joints, and make up the body of the antenna, constitute the so-called funicle. The funicle consists of seven segments unless there are two ring joints in which case there are only six segments in the funicle. The most distal three segments of the antenna form a club which may or may not be enlarged.

The second ring joint which is found in *Ormyrus* is clearly derived from antennal segment four (ordinarily a funicular segment). The number of antennal segments in the family as a whole can be considered constant only if the first ring joint is considered as segment three, and the next segment counted as number four, irrespective of whether it is a normal segment in the funicle, or reduced to a ring joint. In some species this second ring joint is considerably longer and somewhat wider than the first ring joint. In *Ditropinitus* and *Eridontomerus* of the Monodontomerinæ, the first funicular segment (antennal segment four) is smaller than the others, which shows another development of the same tendency toward reduction in this segment. Since there is a tendency in many genera for the funicular segments to become reduced in size, it may be that the first ring joint was likewise derived from a funicular segment.



Antennal characteristics which seem to be of greatest phylogenetic importance are:

1. A definitely clubbed antenna is specialized.
2. An antenna whose funicular segments are notably wider than long departs from the primitive type, and is thus a specialized structure.
3. Greatly enlarged or greatly reduced segments indicate specialization.
4. Antennæ that are reduced in proportion to the body are specialized.
5. Funicular segments which are uniformly cylindrical for their entire length are probably primitive. At any rate, the shape of the funicular segments seems to indicate relationships.

**Callimominæ:** The antenna of *Callimome* (Fig. 14) is usually long in proportion to the body, and although there is sometimes a tendency for a slight club to develop in some species, this is always slight. The male does not exhibit this inclination as much as the female. The first funicular segment is usually slightly longer than the other segments of the funicle, and the segments are longer than wide. The segments are uniformly cylindrical. In the male of some species, the funicular segments are somewhat quadrate.

This same description may be applied to *Diomorus* and *Ecedauma*, but since I possess only two specimens of *Ecedauma*, I cannot generalize too broadly. All these antennæ seem comparatively primitive.

**Monodontomerinæ:** *Zaglyptonotus* (Fig. 15) has an antenna that is essentially the same as that of the Callimominæ except that the segments are more nearly quadrate, and the antenna is shortened. No club is present, and the first funicular segment is slightly the longest of the funicle. The funicular segments are uniformly cylindrical, and subequal. The male antenna is essentially the same except that the funicular segments are more nearly quadrate.

The antenna of *Monodontomerus* (Fig. 19) is much the same as that of *Zaglyptonotus* except that it is not as much reduced in proportion to the body. The antenna of both these genera, while slightly specialized, seem comparatively primitive.

The antennæ of *Ditropinitus* and *Eridontomerus* are modified. In both genera the first funicular segment is the shortest of the funicle, being both shorter and narrower than the normal.

In the female of *Ditropinitus* (Fig. 21) the funicular segments are either wider than long or quadrate, and the segments get slightly wider from the proximal to distal end of the antenna. The segments are somewhat differentiated, each segment being constricted basally. There is no definite club present, but the funicular segments are loosely put together, and the terminal segments are more closely fused, which gives the impression of a club, especially in the female. The female antenna is greatly reduced in proportion to the body. In the male (Fig. 21) the funicular segments are more nearly quadrate, and the first funicular segment is not as much reduced in size as in the female.

In *Eridontomerus* (Fig. 20) the male and female antennæ are essentially alike, and highly specialized. A club is present, and all funicular segments are definitely wider than long. Each segment is constricted basally, and the segments become progressively wider toward the distal end of the antenna. The female antenna is reduced in proportion to the body.

**Megastigminæ:** The antenna of *Megastigmus* (Fig. 16) seems to be comparatively primitive. The male and female are essentially alike; all funicular segments are longer than wide, and are subequal. In some species, the first funicular segment is slightly the longest. No distinct club is present, but in some cases each end of the funicular segments are somewhat rounded. The antennæ are not essentially reduced, and they are relatively slender.

**Ormyrinæ:** The male and female of *Orymrus* (Fig. 18) present specialized antennæ which are essentially alike. Two ring joints are present, and the funicular segments are wider than long. The female antenna is reduced. Each segment of the funicle is constricted basally, and the terminal three segments are more closely fused so that one gets the impression of a club, although this is not greatly enlarged. Because of the reduction of the first funicular segment to a ring joint, the funicle is short in proportion to the scape.

In the female of *Monobaus* (Fig. 24) all segments are consider-

ably wider than long, segmental differentiation is extreme, and the antenna is reduced in length. No definite club is present, but as in *Ormyrus*, one gets the impression of a club. The first funicular segment is considerably shorter than the other funicular segments. The male antenna is essentially the same.

According to the original description of the genus *Monobæus*, only one ring joint is present. But the reduction of the first funicular segment is as great as in some (but not all) species of *Ormyrus*. The validity of the distinction of *Ormyrus* and *Monobæus* has been questioned, and although we must have more material to be certain of this, the character of the ring joints certainly breaks down on occasion.

**Podagrioninæ:** The female of *Podagrion* (Fig. 23) has an antenna with a much lengthened club, and because of this, the whole antenna appears long in proportion to the body. In the funicle, the first funicular segments are longer than wide, and subequal, but in the male (Fig. 22) the first segment is slightly longer than the others. In the female, the most distal of the funicular segments are quadrate. No definite club appears in the male.

In one species of *Podagrion* described by Gahan the club of the female antenna is as long as the whole funicle.

Because of this extreme tendency to club, the antenna of *Podagrion* seems to be greatly specialized. However, the absence of a club in the male is a primitive character.

**Discussion of the Antenna:** The antennal data taken alone supply some evidence of how these callimomid genera are related. All of the Callimominæ, and the genera *Zaglyptonotus*, *Monodontomerus*, (of the Monodontomerinæ) and *Podagrion* (Podagrioninæ) seem to have some relationships. In all these groups the first funicular segment is unreduced, and in most cases is the longest segment of the funicle. With the exception of the female of *Zaglyptonotus*, all of these have antennæ which are not essentially reduced in proportion to the body. In all of these groups, the majority of the funicular segments are longer than wide. The segments are poorly differentiated, so that the joints are hard to discern. In none of these groups, except the female of *Podagrion* is an enlarged club present, and the last three antennal seg-

ments in all the other genera are clearly the prototype of a club.

*Megastigmus* (Megastigminæ) with its reduced antenna, absence of a club, and the first funicular segment which is long in some species is probably related to the above named groups. The more slender antenna may indicate that it is not as closely related to the other groups on this character alone as they are to each other.

*Eridontomerus* and *Ditropinitus* of the Monodontomerinæ seem to be related. In the first named genus, and in the female of *Ditropinitus*, the first segment is distinctly the smallest of the funicle. In both genera, the antennæ are reduced, and segmental differentiation has taken place, especially in *Eridontomerus*. In *Eridontomerus* the funicular segments become widest toward the distal end of the antenna, and in the female of *Ditropinitus* there is a strong tendency toward this condition.

*Ormyrus* and *Monobæus* (Ormyrinæ) seem to be related. There are two ring joints in *Ormyrus*, and a decided tendency for the second ring joint to develop in *Monobæus*. In both, the female antenna is reduced, and segmental differentiation has taken place. All the funicular segments of *Monobæus* are wider than long, and this is true of most of these segments in *Ormyrus*.

*Ditropinitus* and *Eridontomerus* of the Monodontomerinæ seem to have some relationship to *Ormyrus* and *Monobæus*. All these genera have shortened antennæ, and the first funicular segment is the smallest of the funicle. As we shall point out later, however, we are not sure that these apparent relationships are significant.

#### *The Abdomen*

In the clistogastroid Hymenoptera, as is well known, the first true abdominal segment becomes applied to the thorax as the propodeum.

In the chalcidoids, the abdomen is sometimes long petiolate, but in most genera of the Callimomidæ, although there is petiole, it is not prominent.

Recent workers who have studied the morphology of the Callimomidæ and other families of the Chalcidoidea, (James 1926, and Grandi 1930), consider the petiole as a complete abdominal segment. Thus the *first* evident abdominal segment is the *third* true segment.

Counting the propodeum and petiole as true segments, there are nine dorsal plates or tergites in the abdomen of all *Callimomidæ* studied. However, only seven of these are applied to the abdomen proper, and the last one has become modified into the dorsal valves of the ovipositor. Only five true sternites are present in the abdomen proper. If other plates are present they have become considerably modified, and possibly applied to the ovipositor or male genitalia.

In this study the female abdomen was used primarily because the abdomen of the male is more uniform and shows a much greater tendency to shrink. More special structures are present on the female abdomen. In certain cases, however, the male abdomen may be employed to advantage, but unless specified otherwise, all the following descriptions will apply to the female.

The abdominal characteristics which seem to be of greatest phylogenetic importance are as follows:

1. Definite segmentation is more primitive than indefinite.
2. Dorsally incised tergites are specializations.
3. An abdomen with equal segmentation is more primitive than one with some segments enlarged or reduced.
4. An extremely compressed abdomen is specialized.
5. A petiolate abdomen is a specialized structure.
6. Species that have the male and female abdomen nearest alike in size and shape are more primitive than species with greater difference between the sexes.
7. An enlargement of one or more of the sternites is specialization.

It is probable that species in which the posterior sternites can be easily seen laterally are primitive, since this approaches the condition of the primitive abdomen. Likewise, an abdomen in which the sternites are pushed far anterior out of their normal position is presumably specialized. However, since all the abdomens show a certain shrinkage, only those cases in which the above points were extreme could be regarded as significant.

**Callimominæ:** The abdomen of *Callimome* (Fig. 26) is not excessively compressed or petiolate, although some species show this condition more than others. The abdomen is not elongate, and nearly as high as long. The male abdomen is considerably

smaller than the female. In the female, the third true tergite is greatly enlarged and overlaps the fourth, so that it sometimes can scarcely be seen on the mid-dorsal line, although it is more evident laterally. The third tergite is the largest dorsal plate, while the last three tergites are greatly reduced in size. The third and fourth dorsal plates are deeply incised on the posterior edge along the mid-dorsal line. Because of the thinness of the plates, the segmentation dorsally is poorly defined. The two anterior sternites, really sternite three and four, are greatly enlarged and overlap the tergites, and in some cases these are so enlarged that they extend for a great distance posteriorly. This is a remarkable development, not found in very many other Hymenoptera. In a few species the posterior sternites may be seen ventrally, but in others the sterna are enclosed within the tergites.

The above description of the abdomen may be applied to *Diomorus*, except that the anterior sterna are still more enlarged in some species.

*Ecdauma* (Fig. 30) has a very remarkable abdomen for a callimomid. It possesses a true petiole which is very elongate. At the same time it is very compressed. The sterna, however, may be seen ventrally. In other features it shows affinities with the other genera of the Callimominæ.

All these abdomens in the Callimominæ appear well specialized, with that of *Ecdauma* the most highly specialized.

**Monodontomerinæ:** The abdomen of *Zaglyptonotus* (Fig. 31) shows close affinities with *Callimome*. The third tergite is enlarged, incised, and overlaps the fourth. Sternites three and four overlap the tergites, although these are not as enlarged as in some species of *Callimome*. The abdomen is nearly as high as long, and the female abdomen is considerably larger than that of the male. The posterior tergites are reduced in size, while the sternites posteriorly are not visible. This abdomen seems to be specialized.

*Monodontomerus*, (Fig. 27) seems to possess a comparatively primitive abdomen. The segmentation is definite, the abdomen is not compressed or petiolate, the anterior tergites are not incised, although the third tergite overlaps the fourth in the male, and in the female the third tergite is somewhat reduced dorsally.

In one species, however, there is no reduction. The anterior sternites are enlarged only slightly. The male and female abdomen approach each other in size. The last tergites are reduced, and the abdomen is nearly as high as long.

In *Ditropinitus* (Fig. 29) the abdomen seems to be incipiently specialized. The segmentation is indefinite, the third and fourth tergites are incised, and the third tergite is not as enlarged as in the above genera. The anterior sternites are not enlarged, and the abdomen is not compressed or petiolate. The abdomen is considerably elongate and somewhat cylindrical. The size difference between the sexes is considerable.

*Eridontomerus* (Fig. 33) differs from *Ditropinitus* primarily in that the anterior tergites are not incised.

**Megastigminæ:** The abdomen of *Megastigmus* (Fig. 28) seems to be specialized. The abdomen is extremely compressed except in one species, and in this species the male abdomen is depressed and considerably petiolate. In most species, the sterna are all enlarged and these overlap the tergites. The third tergite is enlarged, and incised in all except one species. The last tergites are reduced in size, and segmentation is very indefinite. In most species, the male and female abdomen approach each other in size.

**Ormyrinæ:** In *Ormyrus* (Fig. 34) many species possess several rows of large punctations on the dorsal surface of the median tergites. The females vary somewhat in this feature, but the males almost invariably have these punctations. Dorsally, and part of the way down the sides, the third tergite completely covers the fourth, but further down, the segments are more nearly equal, and both third and fourth are evident. The abdomen is not compressed or petiolate, but in the female it is notably pointed, and cylindrical in shape. The male abdomen is decidedly depressed. The tergites are not incised, and except where the large punctations interfere, the segmentation is definite.

In *Monobæus* (Fig. 38) the abdominal punctations are confined in many species to the anterior margins of the tergites, and since these are overlapped by the plates anterior to them, they cannot be seen externally. In the female, the eighth tergite is bent upward, so that the tip of the abdomen is noticeably tilted. Some species of *Ormyrus* exhibit this characteristic to a less degree.

In the female of *Monobæus*, all the sternites are crowded far anteriorly, so that the posterior one extends only to the fourth tergite. This is certainly a specialization, and since it is so extreme could not be accounted for by shrinkage. In other abdominal features, *Monobæus* shows close affinities with *Ormyrus*.

The abdomen of this subfamily, then, while possessing some primitive features, certainly exhibits some peculiar specializations.

**Podagrioninæ:** The abdomen of *Podagrion* (Fig. 32) seems to be specialized. The female abdomen is extremely compressed, somewhat petiolate, and nearly as high as long. Tergites three and four are greatly enlarged dorsally, incised, and tergite three overlaps tergite four. The last two tergites are reduced in size. The anterior sternites overlap the tergites, and laterally tergite six is the largest plate of the abdomen. In the male, the first tergite and sternite proper are so enlarged that they both extend posteriorly for one half the length of the abdomen. In both male and female segmentation is indefinite while in the two sexes abdominal shape differs radically.

**Discussion of the Abdomen.** From abdominal data alone, we may reach some conclusions as to the relationships among the genera and subfamilies. The Callimominae and the genera *Zaglyptonotus*, *Megastigmus*, and *Podagrion* seem to be related, since in all groups the female abdomen is either greatly compressed or exhibits a tendency toward compression. The anterior sternites overlap the tergites, and there is a tendency for a petiole to develop in all groups. The segmentation is indefinite, and tergite three is enlarged and overlaps tergite four. Both these plates are incised. All the abdomens are nearly as high as long. *Monodontomerus* (Monodontomerinae) seems to be somewhat related to these groups, for the anterior sternites of this genus also show slight inclination to overlap the tergites, while the abdomen is again nearly as high as long. In all these groups, the posterior tergites are reduced in size.

*Eridontomerus* and *Ditropinitus* of the Monodontomerinae show relationship, since in both genera the abdomen is cylindrical, considerably longer than high, and not compressed. In neither genus do the anterior sternites overlap the tergites.



Some indication that these genera may be related to the above groups is found in the indefinite segmentation, the somewhat reduced posterior tergites in both genera, and the incised tergites in *Ditropinitus*.

*Ormyrus* and *Monobæus* of the Ormyrinæ are certainly related to each other. The female abdomen is pointed, the segmentation is definite, the last tergites are not reduced in size, and the male abdomen is decidedly depressed. The anterior tergites are not incised, and the anterior sternites do not overlap the tergites. The peculiar abdominal punctations in *Ormyrus* are duplicated on the anterior part of the tergites in *Monobæus*. The Ormyrinæ do not seem to be closely related to any of the other groups in abdominal characteristics.

#### *Female Genitalia*

The genitalia of the Callimomidæ involve several sets of structures. The ovipositor proper includes the stylets and sheaths. Closely associated with the ovipositor are the dorsal valves which have presumably been derived from the ninth tergum. Hanna (1934) calls these plates the outer plates of Imms, which he states are the same as the quadrate plates of Snodgrass. The ventral valves are termed by Hanna the inner plates of Imms or the oblong plates of Snodgrass. These plates seem to have been derived from the ninth sternum. The fulcral plate of Imms, or triangular plate of Snodgrass, is according to James (1926) an expansion of the basal portion of each stylet. Hanna states that this plate has been derived from the eighth sternum. A thin chitinous plate arises from the dorsal proximal edge of each ventral valve. Grandi (1930), and according to Hanna in an earlier paper, has named this plate the falcate plate.

There is considerable variation among the genera in the length of the ovipositor outside the body, and in the length of the ventral valves. In some genera, there is a tendency for the ovipositor to coil upon itself anteriorly, while in others, the ovipositor and ventral valves outside the body are carried forward at an extreme angle.

The genitalic characteristics which seem of the most importance in phylogenetic interpretation are:

1. Greatly elongate ventral valves outside the body, since they are derived from a portion of a segment, are specialized structures.

2. Basal coiling of the ovipositor is a specialization.

3. External forward bending of the ovipositor and ventral valves as found in one genus is a specialization.

4. Extreme ovipositor length outside the body is a specialization.

5. Any especially enlarged portion of the genitalia whose origin is known to be from the portion of a segment, is evidence of specialization.

**Callimominæ:** In most species of *Callimome* (Fig. 35) the ventral valves and external ovipositor are as long as the body, and in some cases considerably longer. In only a few instances are these structures somewhat shorter than the body. The base of the ovipositor coils upon itself considerably in some species, but in others, this coiling is not as great. In all of the *Diomorus* that I possess the ovipositor and ventral valves are as long or longer than the body, although some species have been described in which these structures are slightly shorter. Basally, the genitalia are essentially the same as in *Callimome*. In *Ecdaua* the ovipositor and ventral valves are nearly twice the length of the body. I did not have enough specimens to study the genitalia basally.

In these structures, all the Callimominæ seem well specialized.

**Monodontomerinæ:** In *Monodontomerus* (Fig. 42) the ventral valves and ovipositor outside the body are considerably shorter than the body. Basally there is not much coiling of the ovipositor, although more than in the following genus.

In *Ditropinitus* (Fig. 39) the ovipositor and ventral valves are very short, and in some instances even shorter than the abdomen. The ovipositor does not coil basally. Both the above genera seem primitive in genitalic features.

I did not possess enough material to study the genitalia basally in *Zaglyptonotus* and *Eridontomerus*. In the first named genus, the external ovipositor and ventral valves are as long as the body. In *Eridontomerus*, however, these structures are shorter than the abdomen. Thus on these features alone, *Eridontomerus* seems primitive while *Zaglyptonotus* is somewhat specialized.

**Megastigminæ:** In some species of *Megastigmus* (Fig. 40) the external ovipositor and ventral valves are longer than the body, while in others these structures are shorter. Basally there is practically no coiling of the ovipositor. Both the dorsal and ventral valves, however, are strongly curved, and externally the ovipositor and ventral valves are curved forward at an extreme angle over the back. In some species of *Callimome* there is a slight tendency for this condition to develop, but the extreme condition seems to be confined to *Megastigmus*. This genus seems specialized in ovipositor features.

**Ormyrinæ:** In both *Ormyrus* (Fig. 41) and *Monobæus* (Fig. 37) the ventral valves and ovipositor hardly extend beyond the tip of the abdomen, although in *Monobæus* they are slightly longer than in *Ormyrus*. Correlated with this shortening of the ovipositor, the base is considerably coiled inside of the abdomen. This condition is more extreme than in any of the other genera, and should therefore be regarded as a specialization; although in a different manner than that found in other genera, where the specialization is found in extreme length development of the ovipositor outside of the body. This basal coiling is more developed in *Monobæus*. In both these genera, the falcate plate is comparatively much larger than in the other genera studied and the external parts of the ventral valves are greater in diameter. In these genera, then, specializations are present, but different from those found in other groups.

**Podagrioninæ:** In *Podagrion* (Fig. 36) those species which I examined possessed ovipositors and ventral valves somewhat longer than the body, although in some described species these structures may be slightly shorter. In a few species, these structures are over twice the length of the body, so that there seems to be a tendency here for extreme length development. Basally there is practically no coiling of the ovipositor. This genus seems specialized, with some species of the extreme length of the ventral valves and external ovipositor highly specialized.

**Discussion of the Ovipositor:** Since in all the Callimominæ, and the genera *Zaglyptonotus* (Monodontomerinæ), *Megastigmus* (Megastigminæ) and *Podagrion* (Podagrioninæ) there is a tendency for the external ovipositor and ventral valves to be as long

as or longer than the body, these groups seem to be related. Extreme basal coiling of the ovipositor is not present in any of these groups. *Eridontomerus*, *Ditropinitus*, and *Monodontomerus* of the Monodontomerinæ seem to be related for in these genera the genetalic ctructures are considerably shorter than the body, and usually shorter than the abdomen. There is no extreme coiling in these genera. *Ormyrus* and *Monobæus* of the Ormyrinæ resemble the last named genera in having shorter ventral valves and ovipositors. But in these genera of the Ormyrinæ, this condition has an entirely different evolutionary significance, because the external shortening of the ovipositor is correlated with internal coiling which is high specialization.

#### *Femora*

In *Podagrion* the hind femur is very much widened and supplied with many large teeth. Indeed the structure is reminiscent of the digging legs of the mole crickets, and a near duplicate of the expanded femora of the Chalcididæ. This development in *Podagrion* is certainly a specialization.

In my collection there are several species presumably of the genus *Callimome* which possess very serrate and somewhat widened hind femora. Otherwise these species show the diagnostic characters of *Callimome*. This similarity of structure seems to indicate that *Callimome* and *Podagrion* are related.

*Eridontomerus* and *Ditropinitus* possess denticulate femora, which taken alone may indicate relationship between these two genera.

The genera *Diomorus*, *Ecdauma*, *Monodontomerus* and *Zaglyptonotus* have a single tooth on the hind femora, and this fact may be indicative of interrelations.

#### *Host Relations*

The following data were obtained in part from the literature, and in part from my own observations. The published data vary much need confirmation as to details, although they may give some indication of the biology of the group.

In dealing with the host relations of any of the families of the Chalcidoidea, many difficulties are encountered. Since the

family *Challimomidæ* is world-wide in distribution, reports of species and of their hosts have appeared in such obscure journals that we can make no pretense of having a complete record of the published material. Then too, the classification of this as well as of the other families of the chalcidoids is so difficult that the published determination of the parasite or of the host, or of both the parasite and host are often incorrect. This is especially true of the older literature, but occurs often enough in the more recent literature because many of the reports of the parasite come from those who are not specialists in the classification of the group.

Probably the most difficult matter in dealing with host relationships is to determine whether a given insect is phytophagous, a mere inquiline, or a true parasite. If it is parasitic, it is not always clear which of the several insects with which it may be associated is the true host. Particularly is this true in dealing with parasites bred from cynipid or other galls where there may be a half dozen other families besides the true gall maker represented in the gall.

While the present summary of host relations is admittedly incomplete, most of the literature has been covered, and it is to be hoped that the most important references studied. When the original references were not available, Dalle Torre's volume in the *Catalogus Hymenopterorum* (Vol. 5) has been of help.

The following tables are designed to give a summary of the host relations of each genus.

So far as I can determine, *Ecdauma* has never been reported from any host.

Although the majority of the species of *Callimome* are parasitic upon Cynipidæ and Itonididæ, several species have been established as phytophagous, and many species have been reported from two and three orders. In one species of *Callimome* both parasitism and phytophagy have been reported.

*Diomorus* which parasitizes only Hymenoptera, seems more restricted.

It has been suggested that *Zaglyptonotus* parasitizes Curculionidæ, but to my knowledge this has not been definitely estab-

## HOST DISTRIBUTION OF CALLIMOMINÆ

Callimomid parasites		Host		
Genus	Species with known hosts	Order	Family	No. of genera parasitized
Callimome	9	Coleoptera	Cerambycidae	1
			Curculionidae	3(?)
			Ipidae	1
			Nitidulidae	1
	82	Diptera	Itonididae	13
			Tipulidae	1
			Trypetidae	4
	5	Homoptera	Aphidae	—
			Chermidae	1
			Cicadidae	2
			Diaspididae	1
	125	Hymenoptera	Argidae	—
			Callimomidae	2
			Chalcididae	1
			Cynipidae	30
			Eurytomidae	3
	6	Lepidoptera	Tenthredinidae	2
Larentiidae			1	
Pyralididae			1	
1	Orthoptera	Tortricidae	2	
		Mantidae	1	
10	Phytophagous	Conifers	1 or 2	
		Dicotyledons	10	
		Monocotyledons	1	
13	Hymenoptera	Crabronidae	1	
		Cynipidae	6	
		Megaehilidae	1	
		Pemphredonidae	1	
		Sphegidae	1	
Diomorus				

## HOST DISTRIBUTION OF MONODONTOMERINÆ

Callimomid parasites		Host		
Genus	Species with known hosts	Order	Family	No. of genera parasitized
Monodontomerus	2	Diptera	Stratiomyidæ	1
	1		Tachinidæ	6
	7	Homoptera	Chermidæ	1
			Hymenoptera	Anthophoridæ
		Apidæ		1
		Braconidæ		3
		Ceratinidæ		1
		Cimbicidæ		2
		Eulophidæ		1
		Ichneumonidæ		6
		Megachilidæ		3
		Tenthredinidæ	2	
	7	Lepidoptera	Lymantriidæ	4
			Lasiocampidæ	3
			Olethreutidæ	1
			Pieridæ	2
			Psychidæ	1
Pyralididæ			1	
Tortricidæ			2	
Zygænidæ	1			
Ditropinitus	1	Diptera	Itonididæ	1
	1	Hymenoptera	Ichneumonidæ	1
			Eulophidæ	1
Eridontomerus	1	Hymenoptera	Eurytomidæ	2
			Eurytomidæ	1

lished.<sup>3</sup> The series which I possess were bred from sunflower heads, and associated with curculionids.

*Monodontomerus* in two instances has been reported from seeds of plants, and these species may be phytophagous, although this

<sup>3</sup> Since the submission of this manuscript for publication, the writer has reared a species of *Zaglyptonotus* from the puparia of *Tephritis finalis* Loew., (Trypetidæ), Curran det.).

has never been established. At least one species of this genus has been definitely known to attack three orders, and many genera in each. Several species have been reported from two orders. As we shall see, however, many species of *Monodontomerus* are hyperparasitic, and it is possible that their true hosts are not what the published records summarized in the above table seem to show.

## HOST DISTRIBUTION OF MEGASTIGMINÆ

Callimomid parasites		Host		
Genus	Species with known hosts	Order	Family	No. of genera parasitized
Megastigmus	1	Coleoptera	Cureulionidæ	1
	5	Diptera	Itonididæ	1
			Trypetidæ	2
	6	Hymenoptera	Cynipidæ	6
	2	Homoptera	Apiomorphidæ	1(?)
	4	Lepidoptera	Gelechiidæ	1
			Pyralididæ	1
			Tineidæ	1
			Tortricidæ	1(?)
	29	Phytophagous	Conifers	9
Dicotyledons			8	

The majority of the species of *Megastigmus* are phytophagous, but several species have been established as parasites, while two have been reported as both parasitic and phytophagous. Many of the phytophagous species occur on hosts of two or more genera, and at least one species has been reported from both a conifer and a dicotyledon. The same is true of some of the parasitic species.

Ormyrus seems to be primarily restricted to Cynipidæ. Several species attack several genera within the Cynipidæ, but only one species has been reported from both a Cynipid and Itonid host.

In many cases the genus of the mantid which was host of *Podagrion* was not determined, but in all authentic cases of parasitism, this genus has been reared only from mantid egg cases.



## HOST DISTRIBUTION OF ORMYRINÆ

Callimomid parasites		Host		
Genus	Species with known hosts	Order	Family	No. of genera parasitized
Ormyrus	30	Hymenoptera	Chalcididæ	1
			Cynipidæ	14
Monobæus	2	Diptera	Itonididæ	1
			1	Hymenoptera

\* *Method of Parasitism.* Although the data upon the method of parasitism within the Callimomidae is indeed fragmentary considering the large number of species with known hosts, some generalizations may be made from a study of these few species. In the following tables, all species that have been adequately studied are listed, and their method of parasitism compared.

Since the genera *Syntomaspis* and *Torymus* are considered as synonyms of *Callimome*, all the above species presumably belong to the genus *Callimome*. *S. pubescens* and *S. elegans* have both been reported as phytophagous and parasitic, but it has been stated that these species are synonyms of *Callimome (Syntomaspis) druparum*.

Since some species of *Callimome* are seemingly able to adapt themselves to a variety of host conditions, they are presumably plastic in their method of parasitism and thus comparatively primitive. Data are not available for the method of parasitism in other genera of the Callimominae.

From these fragmentary data, it seems that at least some species of *Monodontomerus* are hyperparasites, although they may also

## HOST DISTRIBUTION OF PODAGRIONINÆ

Callimomid parasites		Host		
Genus	Species with known hosts	Order	Family	No. of genera parasitized
Podagrion	21	Orthoptera	Mantidæ	6

## CALLIMOME (CALLIMOMINÆ)

Species	Host	Method of Parasitism and stage of host	Authority
<i>C. iris</i>	Mantid	Eggs	Picard 1930
<i>S. oviperditor</i>	Cicada	Feeds externally upon egg masses	Gahan 1927
<i>T. nigricornis</i>	Cynipid, etc.	Any stage, its own or other larvæ. Also hyperparasitic	Picard 1928
<i>C. doryenicola</i>	Itonidid	Internal parasite of larvæ and pupæ	Muller 1870
<i>Torymus</i> sp.	Itonidid	Ectoparasite of larvæ and pupæ	Colizza 1928
<i>Syntomaspis</i> sp.	Cranberry fruit worm	Internal parasite of pupæ	Franklin 1916
<i>Torymus</i> sp.	Dendrolimus	Hyperparasite	Takagi 1925
<i>S. druparum</i>	Many genera of plants and some cynipids	Reported as both parasitic and phytophagous	Several authors

be primary parasites. Those other species that attack the pupæ of their hosts, may also be hyperparasites. However, since some species can seemingly adapt themselves to a variety of conditions, they must be considered primitive. No well founded data are available for other genera of this family.

*Megastigminæ.* As mentioned before, a few species of *Megastigmus* have been reported as both parasitic and phytophagous. A species of *Megastigmus* has been reported as bred from fly larvae, and another from the pupa of its host, but the data are too fragmentary to be used.

*Ormyrinæ.* I have been unable to find any reliable references to the parasitic habits of this subfamily.

*Podagrioninæ.* *Podagrion* has been reported only from mantid egg cases, and thus these parasites seem highly specialized.

**Discussion of Host Relations:** It is rather difficult to compare a genus with a large number of species with one that has

## MONODONTOMERUS (MONODONTOMERINÆ)

Species	Host	Method of Parasitism and stage of host	Authority
<i>M. æreus</i>	Hymenoptera	Larvæ and pupæ	Muesebeck 1931
	Tachinidæ	Puparia	Muesebeck 1931
	Lepidoptera	Pupæ, normally ectoparasitic hyperparasite	Muesebeck 1931
<i>M. dentipes</i>	Pine moth	Hyperparasite	Seitner 1927
	Aporia, Pieris, Lasiocampa	Pupæ	Mayr 1874
	Nematus	Larvæ	Mayr 1874
<i>M. nitidus</i>	Anthophora, Chalicodoma	Pupæ	Mayr 1874
<i>M. obsoletus</i>	Aporia, Psyche	Pupæ	Mayr 1874
<i>M. obscurus</i>	Brachonid	Hyperparasite	Blair 1926

relatively few, since, other things being equal, the genus with the largest number of species might be expected to attack more hosts. However, in comparing two genera with approximately the same number of species, that genus which contains both parasitic and phytophagous species, since it can thus adapt itself to a variety of habits, may be considered more primitive than one containing only parasitic or only phytophagous species. Likewise, those genera which are parasitic upon many families and orders of insects, are physiologically more primitive than those which are more limited in their choice of hosts. The same can be said for the stage of host attacked. Those genera that are limited are presumably specialized.

The question of whether the habit of phytophagy or parasitism is the most recent has been discussed for many years. Gahan (1922) considers that the phytophagous habit is the most recent; that the ancestors of the chalcidoids were plant feeders, that parasitism then developed, and that the present day phytophagous species are of recent origin, and derived from the preceding parasitic species. If this be true, I see no reason why this reversal of habits may not have taken place several times; and even in some instances why the original phytophagous or parasitic tendency

may not have been retained in some instances while a reversal was taking place in others. At any rate, it appears to me that in order to obtain conclusive evidence, one must work out each species separately, since a change of reactions in one group does not necessarily imply that other groups will likewise change.

Some species of *Eurytoma* show both parasitism and phytophagy during their life history. Gahan and Phillips (1927) seem to think that this represents a transition from parasitism to plant feeding. In a phylogenetic study of the Eurytomidæ, Bugbee (MS)<sup>4</sup> thinks that the evidence might be better interpreted as a very generalized physiological state, which seems to be able to adapt itself to either type of feeding; also that fixed parasitism and phytophagy may have emerged as two diverging evolutionary developments, rather than interpreting these species as transitional between parasitism and phytophagy.

The genus *Callimime* with its many species certainly does attack many diverse groups of insect and plants. There are many species that attack as many as three orders, and some species have been reported as both parasitic and phytophagous. Thus, although many species are specialized in their restriction to the Cynipidae and Itonididae, there are other species of *Callimime* that are certainly physiologically primitive. Likewise, some species attack the eggs of their hosts, others may attack several stages, and some species may be hyperparasites or primary, as well as external or internal parasites. Therefore, although some species of this genus seem to be physiologically specialized, there are others that are primitive.

*Monodontomerus*, although known from only a relatively few species, seems to be comparatively primitive, since the known species attack many host groups. Some of the species, however, may be somewhat restricted, since some are hyperparasitic and attack the pupae of their hosts. Some species have been reported from both larvae and pupae of their hosts, but since none have been reported from other stages, they may be somewhat specialized in stage of host attacked, when compared with some species of *Callimime*.

<sup>4</sup> Since the submission of the present paper for publication, Dr. Bugbee's manuscript has gone to press in the Bulletin of the Brooklyn Entomological Society, and will probably appear before this paper.

In number of hosts attacked, some species of *Megastigmus* seem to be somewhat primitive, since many are not generically restricted as to hosts, and some have been reported as both parasitic and phytophagous. The data are too incomplete for us to make assumptions as to the stage of host attacked.

The species of *Ormyrus* for the most part seem specialized in host relations. Only one species has been reported from two orders, and the majority of the species are confined to the Cynipidae. There are no data as to the stage of the hosts which are attacked.

*Podagrion* which seems to be strictly confined in the number of groups attacked, and in the stage of its host, is doubtless highly specialized.

*Callimome* with its many species shows some host duplication with every other genus of the Callimomidae which was studied. Because of the large number of species in *Callimome*, this may or may not be significant. The fact that parasitic and phytophagous species occur only in this genus and *Megastigmus* may indicate that these two groups have somewhat the same physiological tendencies and are related. *Podagrion* and *Callimome* may be somewhat related since a species of *Callimome* attacks mantid egg cases, and with the exception of this species and the Podagrioninae, no other group of the Callimomidae have ever been reared from this host. *Callimome* and *Monodontomerus* seem to be somewhat related, for species of both genera are hyperparasites and external parasites on occasion. Also both genera may attack the pupae of their hosts.

There are some other host duplicates among the genera, but at the present state of our knowledge it is impossible to say whether or not these are significant.

#### PART 2. PHYLOGENETIC POSITION OF GENERA

The detailed analysis of the morphologic structures and the biologic data which allow any interpretation of the phylogenetic position of the callimomid genera, have already been given in Part 1 of the present study. The following account is, therefore, a coordination of the earlier conclusions reached for each of the data studied.

*Callimominae*

**Callimome:** In thoracic and antennal features, this genus seems to be comparatively primitive, but in abdominal and ovipositor characteristics many specializations are present. In their parasitic behavior, some species seem to be restricted, but there are certainly some that are plastic in their reactions. Because of this combination of primitive and specialized features, it seems as though this genus retained many of its ancestral traits while it was specializing other characters. There are some more species within this genus than any other, and since such a variety of biologic reactions are exhibited among the species, it seems as though considerable evolution has taken place within the genus.

As has been pointed out, *Callimome* shows morphologic relationship to the genera *Megastigmus*, *Zaglyptonotus*, *Podagrion*, and to a less degree *Monodontomerus*. Considering the morphologic relationship, it is probable that the apparent biologic relationships between *Callimome* and the above genera may be significant.

**Diomorus:** This genus is certainly closely related to *Callimome*, and it is possible that we are not justified in separating these two genera. Species of this genus show the same general morphologic features and the same relations. In its parasitism, *Diomorus* seems somewhat restricted.

**Ecedauma:** Upon the basis of our limited material, no complete interpretation of this genus can be made. Only one or two species have been described. Judging from the material which I possess, this genus seems to be primitive in antennal features, and somewhat specialized in thoracic characteristics. The extreme length of the external ovipositor and ventral valves seem to be specializations. Because of the extremely petiolate abdomen (the only genus examined with a true petiole) I am inclined to place *Ecedauma* high in the scale of evolution. Although specialized in certain features, this genus still shows relationships to *Callimome* and *Diomorus* within the subfamily.

Huber (1927) does not consider *Syntomaspis* and *Torymus* as genera distinct from *Callimome*. I have so considered these genera in this study.

*Monodontomerinae*

**Monodontomerus:** Morphologically, although this genus possesses slight specializations, it is comparatively primitive. It possesses comparatively few species, but it attacks a variety of hosts, and in this respect seems to be primitive also. Because of these data, I consider *Monodontomerus* as a comparatively primitive genus. As stated before, this genus shows morphologic relationships to the Callimominae. In addition it seems to be somewhat related to *Megastigmus* and *Podagrion*. *Monodontomerus* seems to be closer related to *Zaglyptonotus* than to any other of the genera studied within the Monodontomerinae. Some of the species of *Monodontomerus*, *Callimome*, and *Megastigmus* have the same hosts, and this taken in connection with the morphologic resemblances between the genera may be further indications of relationship.

**Zaglyptonotus:** Although this genus does not present any extreme morphologic specializations, neither does it possess any excessively primitive features, and should for these reasons be considered intermediate in position. *Zaglyptonotus* seems to be more closely related morphologically to *Monodontomerus* than to any other genus studied within the Monodontomerinae. It shows some morphologic relation to the Callimominae, *Megastigmus*, and *Podagrion*. Nothing is known of the biology of the genus.

**Ditropinitus:** This genus also seems to be incipiently specialized, although it does possess certain primitive features in the abdomen and ovipositor. As mentioned before, the group appears to be related to *Eridontomerus*, in antennal, abdominal, and thoracic features. With this in mind, the fact that both these genera parasitize *Harmolita* living in grass stems may be significant. Biologically, *Ditropinitus* seems to be somewhat plastic, although there are no phytophagous species known.

**Eridontomerus:** This genus possesses an antenna as greatly specialized as any genus studied. In other morphologic features, however, it presents both comparatively primitive and specialized characters. It is more closely related to *Ditropinitus* in both biologic and morphologic features, than to any other genus within the Monodontomerinae. Because of the small number of species

with known hosts, no conclusion can be made as to the biology of the genus.

In conclusion, since there are so much difference between the various genera of the Monodontomerinæ, considerable evolution has probably taken place within the subfamily.

#### *Megastigminae*

**Megastigmus.** In antennal features, *Megastigmus* appears to be comparatively primitive, but in abdominal and ovipositor structures highly specialized. In the thorax both primitive and specialized characteristics are present. Biologically, since no great host restriction is shown, the genus is probably primitive. Since both parasitic and phytophagous species are present within the genus, considerable evolution has probably taken place within *Megastigmus*. Morphologically this genus appears to be related especially to the Callimominae, and to the genera *Zaglyptonotus*, *Podagrion*, and to a less degree to *Monodontomerus*. The presence of both phytophagous and parasitic species within *Callimome* and *Megastigmus* suggests biologic relationship between them. Certain host duplications are present between species of *Megastigmus* and *Monodontomerus*, and considering the morphologic resemblances between these genera, this fact is possibly significant.

#### *Ormyrinae*

**Ormyrus:** With the exception of certain presumedly primitive abdominal structures, *Ormyrus* seems to be morphologically specialized. It also appears to be restricted in host relations. Thus I consider this genus as rather highly specialized in both morphologic and biologic features.

**Monobæus:** As before stated, this genus may not be separate from *Ormyrus*. In morphologic features, it is essentially the same as *Ormyrus*, and thus highly specialized. Since nothing of note is known of the biology of the genus, we are not justified in making assumptions.

Although the Ormyrinae as a group show certain resemblances to *Ditropinitus* and *Eridontomerus* within the Monodontomerinæ, I do not believe that this is very significant. The two groups do not duplicate hosts. *Ditropinitus* and *Eridontomerus* seem to be



restricted to insects inhabiting grass, while the Ormyrinae show decided preference for Cynipidæ. Then too, the Ormyrinae possess so many specializations peculiar only to themselves, that I believe that this subfamily should be placed on a separate line of evolution apart from the other subfamilies. Since all the subfamilies presumably came from a common ancestor, certain resemblances are of course to be expected between all groups, but unless these resemblances are many and from a variety of sources, I do not believe we are justified in assuming close relationships.

### *Podagrioninæ*

**Podagrion:** Considering all morphologic and biologic features, *Podagrion* seems to be a very specialized genus. No excessively primitive features are present morphologically, and biologically this genus seems to be by far the most specialized group. As has been pointed out before, *Podagrion* exhibits certain morphological affinities with other groups of the Callimomidæ, namely, the Callimominae, and the genera *Zaglypnotus*, *Megastigmus*, and to a less degree *Monodontomerus*. Considering the morphologic relationship between *Podagrion* and *Callimome*, the fact that a species of *Callimome* has been bred from mantid eggs suggests further connections between these genera. There are no other callimomids known from mantid eggs.

Before concluding a discussion of the phylogenetic position of the genera, a word should be said as to the evolution of the subfamilies. Since many relationships, both morphologic and biologic exist between the genera of the Callimominae, Megastigminae, Monodontomerinae, and Podagrioninae, this seems to indicate that all these subfamilies belong to the same phylogenetic line. At the present state of our knowledge, it is impossible to tell which subfamilies are most closely related. Considering the host connection between *Podagrion* and *Callimome*, and the fact that *Callimome* seems as close or closer to *Podagrion* morphologically than any other group, might indicate that the Podagrioninae are closer related to the Callimominae than to any other subfamily. The presence of both phytophagous and parasitic species in *Callimome* and *Megastigmus* lends evidence to the effect that the Callimominae and Megastigminae may be closely related.

Since the Ormyrinæ do not show close relationships to any of the other subfamilies, it is probable that this group separated from the main line of evolution considerably before the other subfamilies.

#### SUMMARY AND CONCLUSIONS

1. The characteristic which distinguishes the subfamily Callimominæ is a notch on the mesepimeron and not on the mesepisternum.

2. Evidences of relationship based on any single character are not at all dependable, but evidence derived from several sources, both morphologic and biologic, provides a sounder basis for recognizing relationships.

3. A genus in which the species attacks large numbers of insects, or one in which the species are both parasitic and phytophagous, is more primitive than a genus that is more restricted in its host reactions.

4. A genus that is limited to a single stage of host that it attacks, is more specialized than one that attacks many stages.

5. The subfamilies Callimominæ, Monodontomerinæ, Megastigminæ, and Podagrioninæ show interrelations among the genera, and thus seem to belong to the same evolutionary line.

6. The Ormyrinæ probably belong to a different phylogenetic line of evolution.

7. Considerable evolution seems to have taken place within the Monodontomerinæ.

8. All the Ormyrinæ seem to be comparatively specialized both morphologically and biologically.

9. *Podagrion* is highly specialized morphologically, and the most highly specialized genus biologically within the Callimomidæ.

10. Considerable evolution seems to have taken place within the genera *Callimome* and *Megastigmus*.

11. *Monodontomerus* is a comparatively primitive genus both morphologically and biologically.

12. The status of the genera *Diomorus* and *Monobæus*, based upon the currently used distinguishing characteristics, is questionable.

13. Since *Ecdauma* possesses the only abdomen within the Callimomidæ with a true petiole, it should be placed high in the scale of evolution.

14. *Eridontomerus* and *Ditropinitus* seem to be more closely related to each other than to any other genus within the Monodontomerinæ.

15. *Podagrion* and *Megastigmus* are possibly closer related to *Callimome* than to any other genus outside their own subfamily.

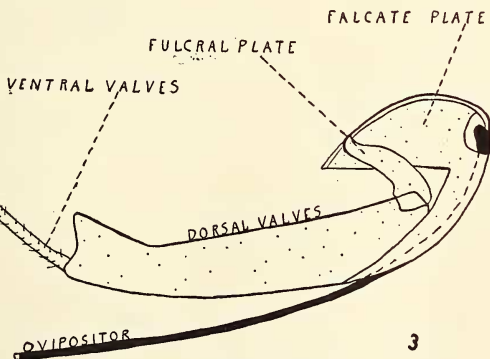
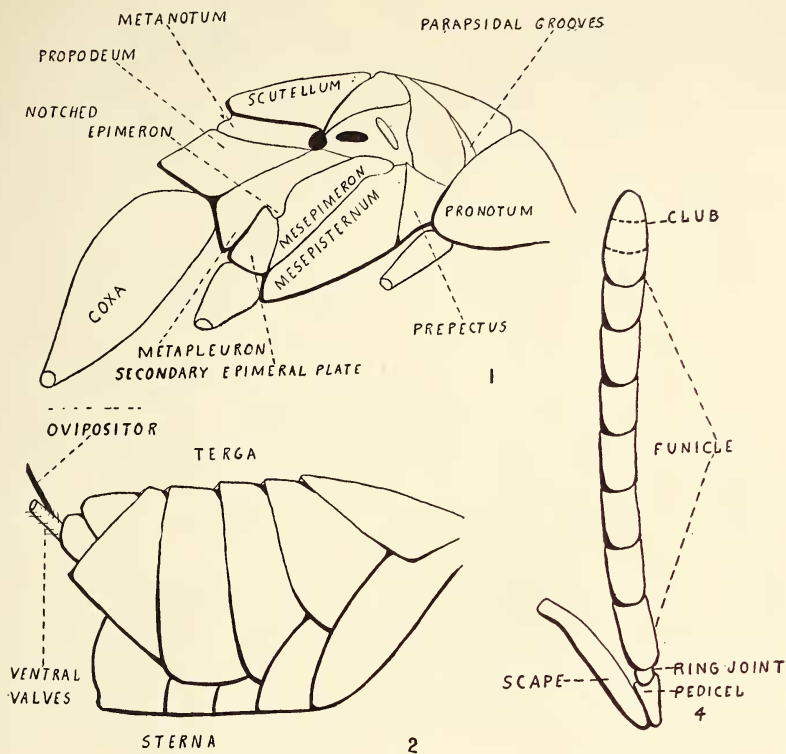
## LITERATURE CITED

- ASHMEAD, W. H. 1896. Phylogeny of the Hymenoptera. Proc. Ent. Soc. Wash. 3: 323-336.
- . 1904. Classification of the chalcid flies. Mem. Carnegie mus. 1 (4): 1-551.
- BLAIR, K. G. 1926. Entomological notes with the Cancer Field Commission in the Trentino, 1925. Journ. Tropic. Medic. and Hyg. 29: 294-98. Reviewed in Rev. App. Ent. (A) 14: 569.
- COLIZZA, C. 1928. Il moscerino delle voile (*Dasyneura affinis* Kieff., Diptera Cecidomyiidae) nell' Italia meridionale. Boll. Lab. Zool. Portici 21: 130-148. Reviewed in Rev. App. Ent. (A) 17: 16.
- CROSBY, C. R. 1913. A revision of the North American species of *Megastigmus* Dal. Ann. Ent. Soc. Am. 6: 155-170.
- CUSHMAN, R. A. 1917. Two new chalcids from seed of *Amelanchier*. Proc. Ent. Soc. Wash. 19: 79-86.
- DALLE TORRE, C. G. 1898. Catalogus Hymenopterous, vol. 5: Chalcididæ et Proctotrupidæ: 281-315.
- FOERSTER, A. 1856. Hymenopterologische Studien 2: Chalcididæ und Proctotrupii. Pp. 1-151. Aachen von Meer.
- FRANKLIN, H. J. 1916. Report of cranberry substitution for 1915. Mass. Agric. Exp. Sta. Bull. 168.
- GAHAN, A. B. 1927. A new species of *Syntomaspis*. Proc. Ent. Soc. Wash. 29: 99-100.
- . 1922. A list of phytophagous Chalcidoidea with descriptions of two new species. Proc. Ent. Soc. Wash. 24: 33-58.
- . 1933. The serphoid and chalcidoid parasites of the Hessian fly. U. S. Dept. Agric. Misc. Publ. 174.
- GIRAULT, A. A. 1915. Australian Hymenoptera Chalcidoidea 9. Mem. Queensland Museum 4: 275-313.
- GRANDI, G. 1930. Monografia del gen. *Philotrypsis* Först. Boll. del Lab. di Entomologia 3: 1-181.
- HANNA, A. D. 1934. The male and female genitalia and the biology of *Euchalcidia caryobori* Hanna (Hymenoptera, Chalcidinae). Trans. Royal Ent. Soc. London 82: 107-136.
- HUBER, L. L. 1927. A taxonomic and ecological review of the North

- American chalcid-flies of the genus *Callimome*. Proc. U. S. Nat. Mus. 70 (14): 1-114.
- JAMES, H. C. 1926. The anatomy of a British phytophagous chalcidoid of the genus *Harmolita* (*Isosoma*). Proc. Zool. Soc. London 1: 75-182.
- MAYR, G. 1894. Der Europäischen Torymiden. Verhandl. Zool.-Botan. Gesel. Wien 24: 53-142.
- MUESEBECK, C. F. W. 1931. *Monodontomerus æreus* Walker, both a primary and secondary parasite of the brown-tail moth and the gypsy moth. Journ. Agric. Res. 43: 445-460.
- MULLER, A. 1870. A preliminary account of *Cecidomyia doryenii* spec. nova and of *Callimome dorynicola* spec. nova, its parasite. Ent. Month. Mag. 1870: 76-77.
- PHILLIPS, W. J. 1927. *Eurytoma parva* (Girault) Phillips and its biology as a parasite of the wheat joint worm, *Harmolita tritici*, Fitch. Journ. Agric. Res. 34: 743-758.
- PICARD, F. 1928. Le parasitisme et l'hyperparasitisme chez le *Torymus nigricornis* (Hym. Chalcididæ). Bull. Soc. Ent. France 1928: 109-111.
- . 1930. Sur deux hyménoptères chalcides nouveaux, parasites dans des oöthèques de mantides. Bull. Soc. Ent. France 1930: 87-90.
- SCHMEIDEKNECHT, O. 1909. Genera Insectorum, 97, Hymenoptera, Chalcididæ. P. Wystman, Bruxelles, Pp. 1-550.
- SEITNER, M. 1927. Aus der Praxis der Kiefernspinnerbækämpfung. Zeitschr. Angew. Ent. 12: 428-435. *Reviewed in* Rev. App. Ent. (A) 15: 383.
- SNODGRASS, R. E. 1911. The thorax of the Hymenoptera. Proc. U. S. Nat. Mus. 39: 37-91.
- TAKAGI, G. 1925. Studies on the methods for the control of *Dendrolimus spectabilis*, Butl. (*Lasiocampidæ*). Forest Exp. Sta. Rept. 2: 1-72. *Reviewed in* Rev. App. Ent. (A) 15: 220.
- WESTWOOD, J. O. 1829. On the Chalcididæ. Zool. Journal 4: 3-32.

## PLATE XXV

- Structures of *Callimomidæ* showing principal parts
- Figure 1. Thorax of *Callimomidæ* (*Callimominæ*)
- Figure 2. Abdomen of *Callimomidæ*
- Figure 3. Female genitalia of *Callimomidæ*
- Figure 4. Antenna of *Callimomidæ*

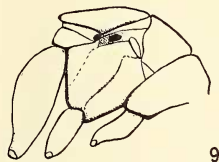
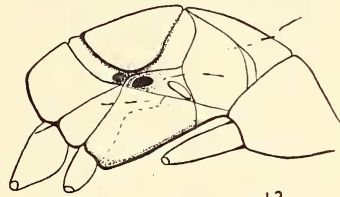
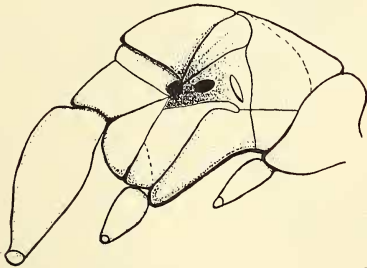
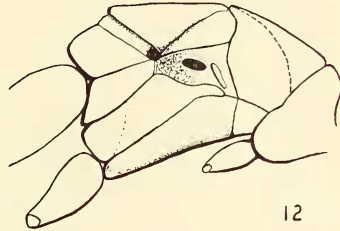
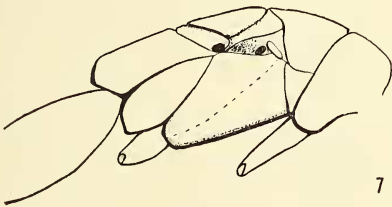
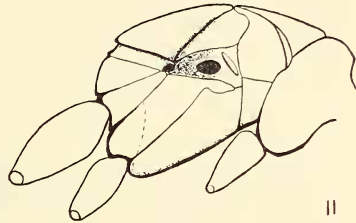
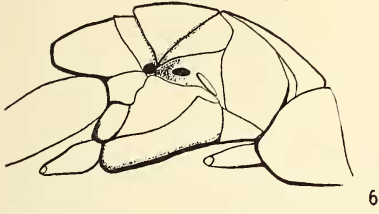
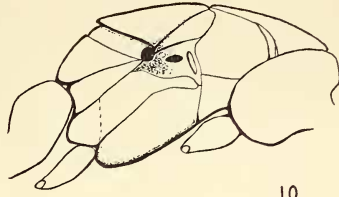
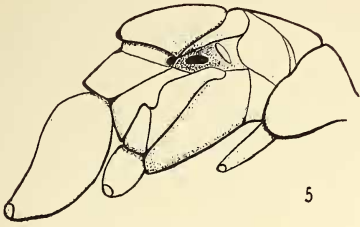


CALLIMOMIDÆ

## PLATE XXVI

(From adults uniformly enlarged to 200 mm. so that the relative size of thoraces may be compared by direct comparison of thorax drawings).

- Figure 5. Thorax of *Callimome* sp.
- Figure 6. Thorax of *Ecedauma* sp.
- Figure 7. Thorax of *Podagrion* sp.
- Figure 8. Thorax of *Monodontomerus* sp.
- Figure 9. Thorax of *Ormyrus* sp.
- Figure 10. Thorax of *Eridontomerus* sp.
- Figure 11. Thorax of *Ditropinitus* sp.
- Figure 12. Thorax of *Zaglyptonotus* sp.
- Figure 13. Thorax of *Megastigmus* sp.



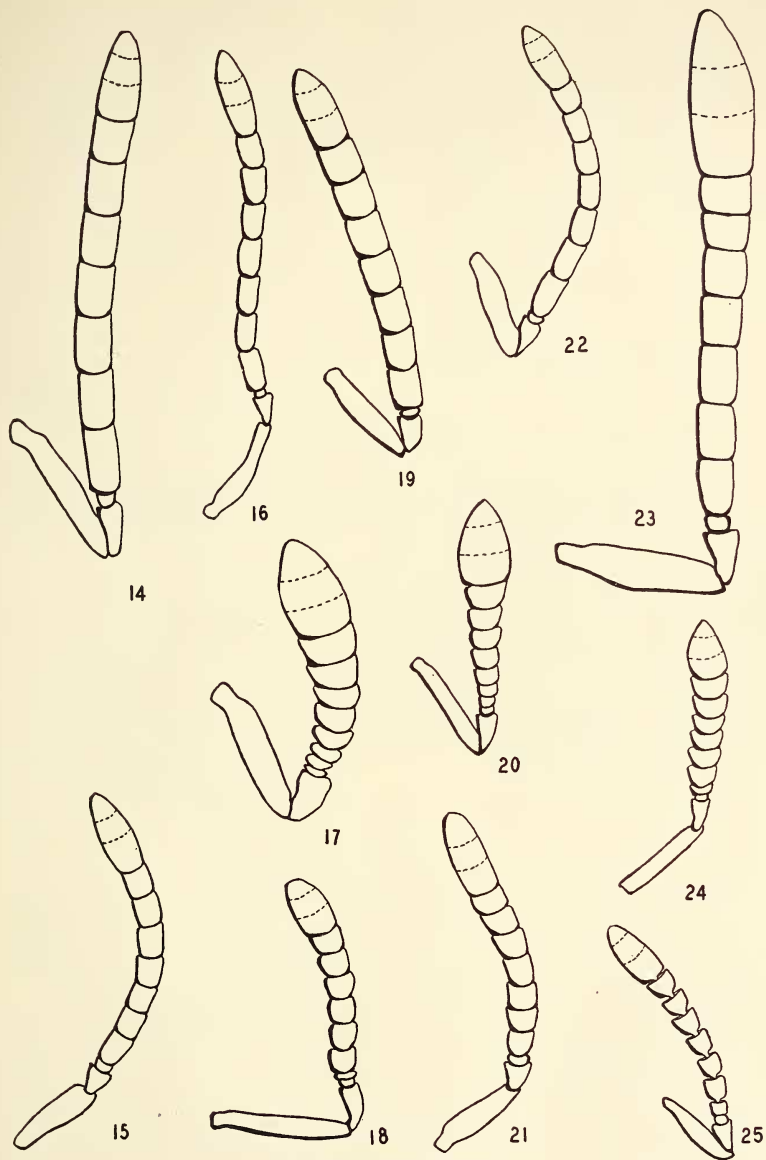
CALLIMOMIDÆ

## PLATE XXVII

(From adults uniformly enlarged to 350  $\mu$ m. so that the antenna-body ratio may be compared by direct comparison of drawings).

- Figure 14. Antenna of female of *Callimome* sp.
- Figure 15. Antenna of female of *Zaglyptonotus* sp.
- Figure 16. Antenna of female of *Megastigmus* sp.
- Figure 17. Antenna of male of *Eridontomerus* sp.
- Figure 18. Antenna of female of *Ormyrus* sp.
- Figure 19. Antenna of female of *Monodontomerus* sp.
- Figure 20. Antenna of female of *Eridontomerus* sp.
- Figure 21. Antenna of male of *Ditropinitus* sp.
- Figure 22. Antenna of male of *Podagrion* sp.
- Figure 23. Antenna of female of *Podagrion* sp.
- Figure 24. Antenna of female of *Monobaeus* sp.
- Figure 25. Antenna of female of *Ditropinitus* sp.



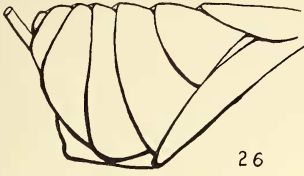


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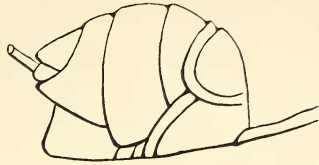
## PLATE XXVIII

(From adults uniformly enlarged to 200 mm. so that the relative size of the abdomen may be compared by direct comparison of abdominal drawings).

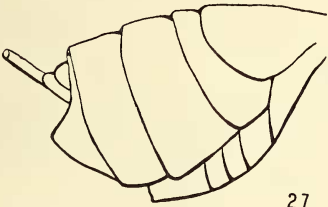
- Figure 26. Abdomen of *Callimome* sp.
- Figure 27. Abdomen of *Monodontomerus* sp.
- Figure 28. Abdomen of *Megastigmus* sp.
- Figure 29. Abdomen of *Ditropinitus* sp.
- Figure 30. Abdomen of *Eedauma* sp.
- Figure 31. Abdomen of *Zaglyptonotus* sp.
- Figure 32. Abdomen of *Podagrion* sp.
- Figure 33. Abdomen of *Eridontomerus* sp.



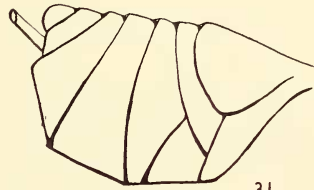
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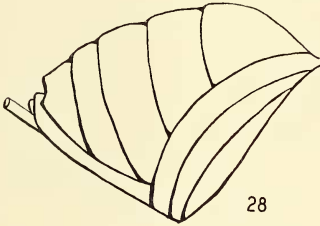
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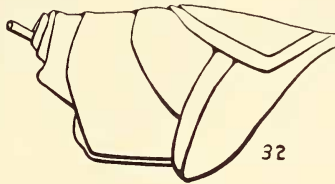
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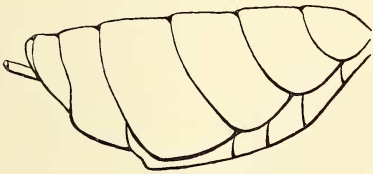
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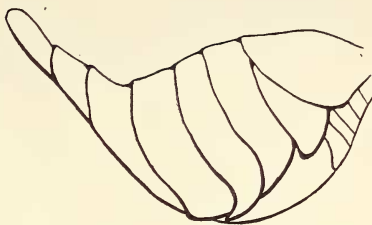
## PLATE XXIX

(Figs. 34 and 38 from adults uniformly enlarged to 200 mm. Other figures from adults uniformly enlarged to 125 mm. so that comparative size of parts may be compared by direct comparison of genitalie drawings).

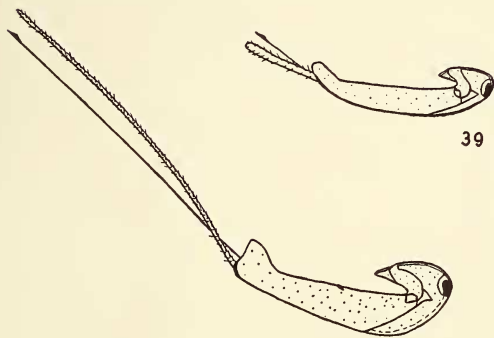
- Figure 34. Abdomen of Ormyrus sp.
- Figure 35. Female genitalia of Callimome sp.
- Figure 36. Female genitalia of Podagrion sp.
- Figure 37. Female genitalia of Monobæus sp.
- Figure 38. Abdomen of Monobæus sp.
- Figure 39. Female genitalia of Ditropinitus sp.
- Figure 40. Female genitalia of Megastigmus sp.
- Figure 41. Female genitalia of Ormyrus sp.
- Figure 42. Female genitalia of Monodontomerus sp.



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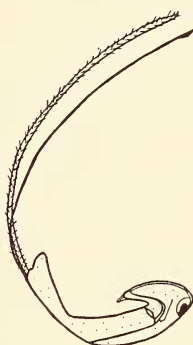
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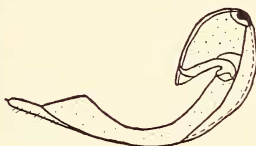
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